

Tree size, exposure, and hydraulic traits interactively shape drought response in a temperate broadleaf forest

Ian McGregor, Ryan Helcoski, Norbert Kunert, Alan Tepley, Valentine Herrmann, Joseph Zailaa, Atticus Stovall, Neil Pederson, Lauren Sack, Krista Anderson-Teixeira

Abstract

content from AGU abstract: Here, we integrate forest census data from a 25.6-ha ForestGEO plot in Virginia (USA), tree-ring records for 12 species representing ##% of woody productivity, leaf hydraulic trait measurements, and microhabitat data. Individual-level growth responses to three droughts (1964-66, 1977, 1999) were stronger among taller trees in dominant canopy positions, those in wetter microsites, and for more drought-sensitive species as assessed by leaf traits (turgor loss at less negative leaf water potential, greater shrinkage with leaf dehydration), with substantial variation in the best predictor variables across given droughts. We conclude that when droughts occur, large dominant trees, drought sensitive species, and individuals in moist microhabitats are likely to be most strongly affected.

Introduction

Understanding how and why trees respond to drought is critical to predicting forest drought responses and climate change feedbacks.

Forests are diverse in terms of tree sizes and functional traits, and it is known that trees varying in size and functional traits respond differently to drought (e.g., (Bennett et al., 2015); REFS). Therefore, in order to understand whole-forest response to drought, we need to know how responses vary by tree size/ species. To do so, there are four fundamental questions that must be addressed:

First, how significant is the effect of individual drought years? Droughts are rarely explicitly defined in ecological studies (Slette et al., 2019), yet no two droughts are the same. This study addressed this by analyzing trees' resistance to drought within and across three defined drought periods.

Second, what drives the observed tendency for large trees to suffer more during drought?

(Bennett et al., 2015) showed that in forests globally, large trees suffer greater growth reductions during drought. However, this analysis quantified tree size based on DBH, which has no direct mechanistic meaning. This study proposed three major mechanisms (besides insects): (1) inherently greater biophysical challenge of being tall; (2) greater exposure of the crowns of large trees; and (3) greater water availability. It is also expected that roots play a role, though these hypotheses still need to be tested.

Third, how do species' traits influence drought response? Analyzing drought responses on the species level does not fully explain mechanisms and is not feasible in diverse forests. The solution is a trait-based approach. Leaf hydraulic traits hold more promise than more commonly/traditionally-measured traits such as wood density and SLA (Medeiros et al.).

Fourth, how do tree size and functional traits interact to influence drought response? It is possible that the pattern observed by (Bennett et al., 2015) could be caused by smaller trees being more drought resistant. Alternatively, larger trees may have more drought-resistant traits as adaptations to greater biophysical challenges.

Hypotheses

1. How significant are individual drought years on a long time-frame trend? 1.1 Individual drought scenario is a strong predictor of drought stress.

* P1.1 - Drought stress is proportional to the severity of each drought.

2. Why do larger trees suffer greater growth declines during drought? Our forest displays the same trend as most forests globally (Bennett et al., 2015). (Note that Bennett et al. 2015 identified only one study on tree growth responses to drought in the Eastern US temperate deciduous biome. We know little about how tree size shapes drought response in this biome.)

2.1 DBH is a strong predictor of drought stress.

- * P2.2-Drought response increases with DBH at time of drought.

2.2. Height is a strong predictor of drought stress.

- * P2.2-Drought response increases with height at time of drought.

- * P2.2a - Drought response is better predicted by height than DBH.

2.3. Large trees suffer more during drought because of greater exposure (to radiation, wind, etc.)—either in relation to neighboring trees or because of position on landscape.

- * P3.1- Trees currently in a dominant canopy position suffered more during drought.

2.4. Rooting volume/depth relative to water sources are critical in drought response. Effects of drought on larger trees are mediated by the fact that large trees have better access to water.

- * P3.2- drought response increases with topographic wetness index

3. Do species functional traits predict drought response?

- * P3.1 - diffuse porous species are more sensitive than ring porous (previously observed in eastern de

- * P3.2 - higher percent leaf area predicts higher drought stress

- * P3.3 - higher leaf mass area correlates positively to drought resistance (more sclerophyllous vegeta

- * P3.4 - TLP correlates negatively with drought resistance (NEVER tested),

- * P3.5 - higher wood density means more drought resistant

4. How are functional traits distributed across size classes, and how does this affect size-resistance relationship?

4.1. Larger/ more exposed trees have more drought resistant traits, meaning size effects are buffered by traits

4.1_alt. Larger trees suffer more because they have more drought vulnerable traits.

- * P3.1a- TLP is lower (larger negative) in taller/canopy trees

- * P3.1b- diffuse porous species more common in understory

- * P3.2- Inclusion of TLP / rp in model does not eliminate or significantly reduce effect of tree size.

I think for #4 here the focus should be on hypotheses looking at the overall trend compared to the specific scenarios?

4. How do droughts vary in their affect on tree resistance?

- * P4.1 - The combined-years scenario will have more explaining variables than the individual scenarios.

- * P4.2 - Inclusion of leaf hydraulic traits does not eliminate or significantly reduce effect of tree s

- * P4.3 - Drought resistance for each scenario will be explained more by hydraulic traits than by the bi

Methods

Study site Research was conducted at the 25.6 ha ForestGEO (Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78° 08'43.4"W) (Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains at the northern edge of Shenandoah National Park. Elevations range from 273-338m above sea level (Gonzalez-Akre et al., 2016) with a topographic relief of 65m (Bourg et al., 2013). Dominant species include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.).

Data collection and preparation The SCBI ForestGEO plot was censused in 2008, 2013, and 2018 following standard ForestGEO protocols... [DETAILS]. Here, we use ... (*very brief summary of which data we use for what purpose— but some will be better integrated with methods descriptions below*)

We analyzed tree-ring data from the twelve species contributing most to woody aboveground net primary productivity (ANPP_stem) (Table 1), which together comprised 97% of whole-ecosystem ANPP_stem between 2008 and 2013. Cores were collected in 2010-2011 or 2016-2017 from a breast height of 1.3m using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees were selected at random from each species in 2010-2011, with at least 30 of those trees having a diameter at breast height (DBH) of at least 10cm (Bourg et al., 2013). In 2016-2017, cores were collected from all dead trees found in the annual mortality census (Gonzalez-Akre et al., 2016). Cores were sanded, measured, and cross-dated using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies have been published in association with (Helcoski et al., 2019): (GitHub URL), (ITRDB).

Height measurements (n=# trees) were taken by several researchers between 2012 to 2019, and are archived in a public GitHub repository (*GitHub URL*). Measurement methods included manual (Stovall et al., 2018a, NEON), digital rangefinders (Anderson-Teixeira et al., 2015b), and automatic LiDAR (Stovall et al., 2018b). Rangefinders either used the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. The associated errors for using either method were acknowledged (Larjavaara and Muller-Landau, 2013). Species-specific height allometries were developed (Table S# - **ADD THIS TABLE TO SI**). For species that didn't have enough height measurements, heights were calculated from equations derived from all species in the study.

For each tree, we combined tree-ring records and allometric equations of height and bark thickness to retroactively calculate DBH and estimate height for the years 1950-2009. Prior DBH was estimated using the following equation, using 2008 as the earliest year for having reliable DBH measurements:

$$diamYEAR = dbh2008 - 2 * (bark.depth2008) - 2 * \Sigma(ring.widthYEAR : ring.width2008) + 2 * (bark.depthYEAR)$$

Here, *ring.width* was measured from cores. Bark thickness was estimated from species-specific allometries based on the bark thickness data of (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression equations on log-transformed data to relate bark thickness to DBH (Table S#- **create table to give these equations in SI**) and then used these to estimate bark thickness based on DBH.

Crown positions were recorded in the field during the growing season of 2018 following the crown position protocol from (Jennings et al., 1999), whereby positions were ranked as dominant, codominant, intermediate, or suppressed. As there was no way to retroactively estimate crown position, we assumed that 2018 crown position was reflective of each tree's position over the past 60 years. While some trees undoubtedly changed position, an analysis of crown position relative to height (Fig. XX) and height change since 1959 indicated that change was likely slow. [**work on this— provide details?**]

Topographic wetness index (TWI) was calculated using the (Metcalf et al., 2018) package in R.

Hydraulic traits were collected from SCBI and are summarized in Table 1. In August 2018, we collected leaf samples from three individuals of each species ... (**Nobby's description of methods for the following**)
1. PLA 2. LMA 4. Wood density 5. TLP

Table 1. Species analyzed here, listed in descending order of ANPP_stem. n cores and DBH range represented, and species traits [*This replaces/combines the two remaining tables in this section. Suggested columns, with those to include only if they fit in parentheses: species, (stems ≥ 10 cm per ha in plot), (ANPP_stem), n cores, DBH range of cores, (n cores in each crown position) species means for each trait]

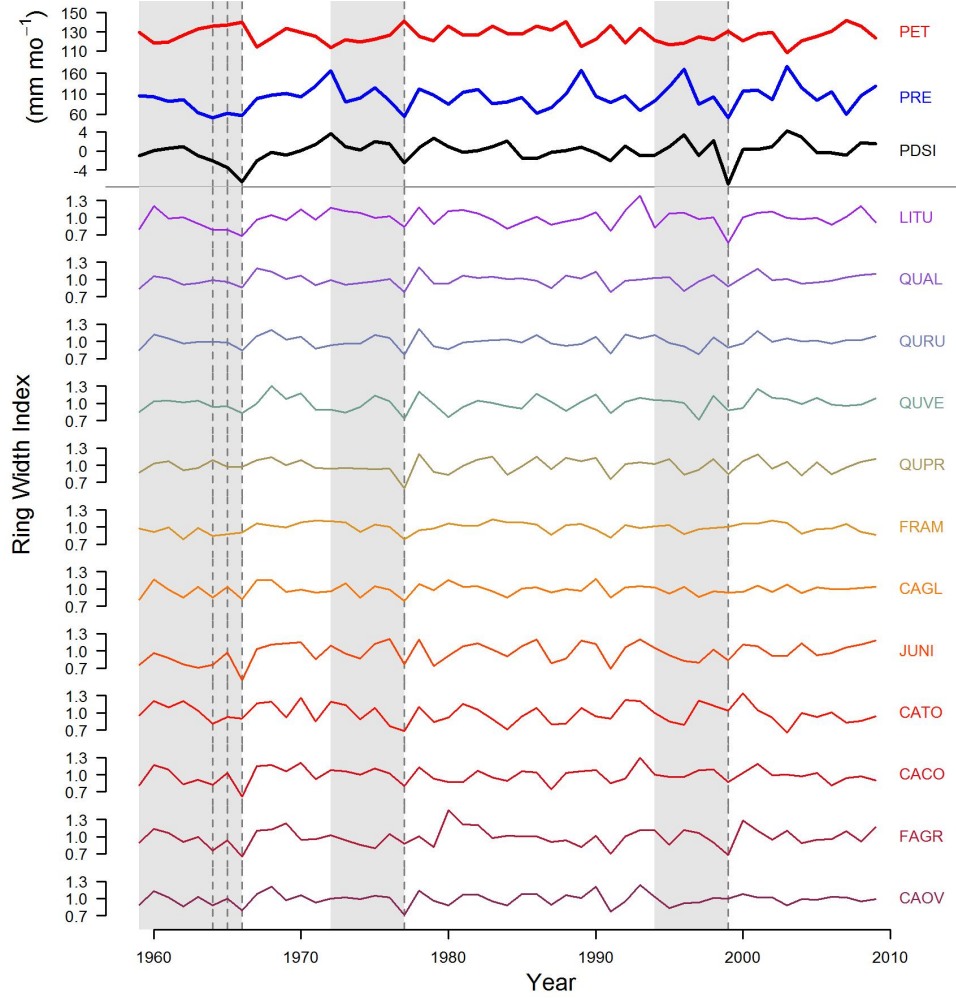
sp	n_cores	dominant	co-dominant	intermediate	suppressed	prior dead
caco	13	NA	2	5	5	1
cagl	31	1	8	16	5	1
caovl	23	4	5	12	2	NA
cato	13	NA	NA	6	2	5
fagr	80	NA	7	48	25	NA
fram	62	NA	17	19	14	12
juni	31	NA	21	8	NA	2
litu	98	9	29	25	30	5
qual	61	4	34	20	3	NA
qupr	59	1	26	20	12	NA
quru	69	6	36	23	2	2
quve	77	6	46	22	1	2

Trait	Unit	mean	min	max
Ring Porosity	ring, semi-ring, diffuse	NA	NA	NA
Percent Leaf Area	%	15.09	8.52	24.64
Leaf Mass Area	g/m ²	53.50	30.68	75.80
Wood density	g/cm ³	0.70	0.40	1.09
TLP	MPa	-2.36	-2.76	-1.92

Climate and drought years [add description of climate data used in Fig. 1, NEON vertical profiles]

To accurately understand climate sensitivity, this study used a specific definition of drought, which is not a common practice (Slette et al., 2019). We used the pointRes package (van der Maaten-Theunissen and van der Maaten, 2016) in R (version 3.5.3) to determine drought periods based on trees' drought resistance, which is defined by (Lloret et al., 2011) as the ratio between the performance during and before the disturbance. Candidate drought years were defined if $>50\%$ of the cored trees experienced $<30\%$ growth in a year compared to the previous 5 years. These were then cross-validated with the regional Palmer Drought Severity Index (PDSI) values for each year, which yielded a set of three periods that were consistently shown as drought: 1964-1966, 1977, and 1999.

Figure 1. Time series of peak growing season (May-August) climate conditions and residual chronologies for each species. Droughts analyzed here are indicated by dashed lines, and shading indicates the pre-drought period used in calculations of the resistance metric. Figure modified from (Helcoski



et al., 2019).

Results

Once the data was collected, linear mixed models were run following the order of the hypotheses as seen in Figure ??? [individual_tested_traits]. Using the (van der Maaten-Theunissen and van der Maaten, 2016) package, we set up models with the resistance value as the response variable, and each prediction's variable as the independent variable. Variables' importance in predicting drought tolerance was calculated from mixed-effects models and the lowest AICc (Bates et al., 2019, Mazerolle and portions of code contributed by Dan Linden. (2019)). Null models were determined in order of the predictions. First, we analyzed the combined scenario to determine if "year" was significant. Upon establishing this, we tested height and DBH as size parameters. Although both were significant, height was kept due to its larger delta AICc compared with the null model. We then tested the remaining biophysical and hydraulic traits individually against a null model containing height and year. This yielded Figure ??? (cand_full). All variables with dAICc >2 were used as candidates for each scenario's best model (figure ??? (tested_traits_best))

Table 1: All variables tested for climate sensitivity against appropriate null models, in line with hypothesis predictions. Each variable was tested for each drought scenario excepting "year"

prediction	variable	variable_description	null_model	tested_model
1.1	year	drought.year	resist.value ~ (1 sp/tree)	resist.value ~ (1 sp/tree)+year
2.1	dbh.ln.cm	ln[DBH]	resist.value ~ year+(1 sp/tree)	resist.value ~ year+(1 sp/tree)+dbh.ln.cm
2.2	height.ln.m	ln[height]	resist.value ~ year+(1 sp/tree)	resist.value ~ year+(1 sp/tree)+height.ln.m
3.3	position_all	crown.position	resist.value ~ height.ln.m+year+(1 sp/tree)	resist.value ~ height.ln.m+year+(1 sp/tree)+position_all
3.4	TWI	topographic.wetness.index	resist.value ~ height.ln.m+year+(1 sp/tree)	resist.value ~ height.ln.m+year+(1 sp/tree)+TWI
4.1	rp	ring.porosity	resist.value ~ height.ln.m+year+(1 sp/tree)	resist.value ~ height.ln.m+year+(1 sp/tree)+rp
4.2	PLA_dry_percent	percent.leaf.area	resist.value ~ height.ln.m+year+(1 sp/tree)	resist.value ~ height.ln.m+year+(1 sp/tree)+PLA_dry_percent
4.3	LMA_g_per_m2	leaf.mass.area	resist.value ~ height.ln.m+year+(1 sp/tree)	resist.value ~ height.ln.m+year+(1 sp/tree)+LMA_g_per_m2
4.4	mean_TLP_Mpa	mean.turgor.loss.point	resist.value ~ height.ln.m+year+(1 sp/tree)	resist.value ~ height.ln.m+year+(1 sp/tree)+mean_TLP_Mpa
4.5	WD_g_per_cm3	wood.density	resist.value ~ height.ln.m+year+(1 sp/tree)	resist.value ~ height.ln.m+year+(1 sp/tree)+WD_g_per_cm3

Table 2: Candidate variables to be included in full model, chosen by $dAICc > 2$ when individually tested against a null model

prediction	variable	variable_description	top_model
1.1	year	drought.year	all
2.2	height.ln.m	ln[height]	all
2.2	height.ln.m	ln[height]	1966
3.3	position_all	crown.position	1999
3.4	TWI.ln	topographic.wetness.index	all
3.4	TWI.ln	topographic.wetness.index	1977
3.4	TWI.ln	topographic.wetness.index	1999
4.1	rp	ring.porosity	1999
4.2	PLA_dry_percent	percent.leaf.area	all
4.2	PLA_dry_percent	percent.leaf.area	1966
4.4	mean_TLP_Mpa	mean.turgor.loss.point	all

Table 3: Best full models for each drought scenario

best_model	r2	scenario
resist.value ~ year+height.ln.m+position_all+TWI+PLA_dry_percent+mean_TLP_Mpa+(1 sp/tree)	0.13	all droughts
resist.value ~ height.ln.m+rp+PLA_dry_percent+(1 sp)	0.24	1964-1966
resist.value ~ TWI+rp+mean_TLP_Mpa+(1 sp)	0.21	1977
resist.value ~ height.ln.m+position_all+TWI+rp+PLA_dry_percent+(1 sp)	0.25	1999

Discussion

1. paragraph summarizing main results -> primary conclusions When including only biophysical traits, trees' resistance value (on a per-species basis) is explained best by crown position and height, with codominant trees being the most resistant to drought. This follows on work done by (Bennett et al., 2015) [and others?] which show that larger trees suffer more during drought, and confirms that this susceptibility can be seen in tree ring analyses. Adding in crown position with the leaf hydraulic traits yields a slightly worse predictive model for drought tolerance, with height remaining as the only significant biophysical variable.

We partially supported the hypothesis that crown exposure makes trees more vulnerable to drought. Codominant trees had the highest drought resistance. Dominant trees had lower resistance, likely because they are the most exposed. Other studies have found clear evidence of greater drought sensitivity in trees with exposed crowns (e.g., (Suarez et al., 2004); (Scharnweber et al., 2019)). At the same time, intermediate and

suppressed trees had even lower resistance. This indicates that other mechanisms such as competition or rooting depth were important. (Also note that our study design was not ideal for testing the role of canopy position. Current canopy position is a conservative separator of canopy position: trees may currently be in more dominant positions than they were at the time, but backwards movement is unlikely. This would bias against finding a significant effect for H1.2. Height may be a more reliable predictor of past canopy position than is current canopy position, and explains a portion of variation in canopy position.)

Proximity to stream—either vertical (elev) or horizontal (distance)— did not increase drought resistance; rather, it tended to decrease resistance (H1.3a). This may be because individuals growing further from water are acclimatized to drier conditions. However, the increase in drought resistance with distance from stream was less for small than large trees (H1.3b), indicating a potential importance of root depth/volume in conferring drought resistance.

misc content to integrate From (Kannenberget al., 2019), species with diffuse porous wood anatomy (*Liriodendron*) are more sensitive to drought, whereas ring-porous are not as affected because they more easily rebuild structures for hydraulic conductivity. This paper mentions it would be good to have this data with respect to latent affects from drought. ### Conclusion words ### Supplementary Information

SCBI ForestGEO Plot

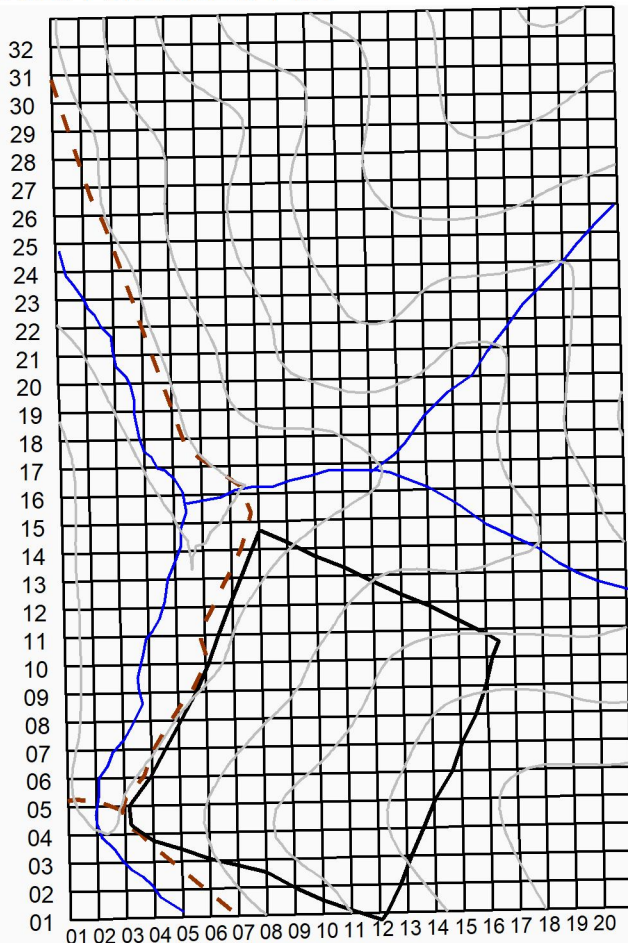


Figure 1: Map of ForestGEO plot

p50 and p80 We decided to include values of P50 and P80 in the leaf traits model, defined by (Anderegg

et al., 2016) as the water potentials at which a species loses 50% and 88% [80% by proxy], respectively, of hydraulic conductivity. Values were calculated by (**insert new methods here??**), and were only available for six species (*C. glabra*, *L. tulipifera*, *Q. alba*, *Q. prinus*, *Q. rubra*, and *Q. velutina*). Because of this, the model runs were considered to be incomplete due to the exclusion of the other 8 species. Results revealed neither p50 nor p80 to be significant, thus for the full analysis we decided to drop the two traits in order to include all species in the full analysis.

(see Issue #32)

include TWI by trait graphs (2) here

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